

GABBRO SOIL-PLANT RELATIONS IN THE CALIFORNIA FLORISTIC PROVINCE

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ABSTRACT

The paper reviews published botanical and pedological literature concerning gabbro in the California Floristic Province. Gabbro is a mafic plutonic rock that is common in the Sierra Nevada, Klamath Mountains, and Peninsular Ranges of the California Floristic Province. Its mineralogical and chemical compositions span the range between those of peridotite, an ultramafic rock, and diorite, a rock more silicic than gabbro. A broad range of nutrient element compositions makes gabbro soils extremely diverse substrates that harbor numerous rare and endemic plant species, particularly at the Pine Hill intrusive complex in El Dorado County, California. Several directions for further work are also suggested. More research is required to discern the poorly understood factors affecting endemism and plant distributions on gabbro soils. Attention should be paid to floristic differences between olivine gabbro, which chemically borders serpentine, and gabbro lacking olivine or containing more hornblende than olivine. A species list is provided which highlights rare, serpentine-preferring, and gabbro-endemic taxa reported from gabbro soils in the California Floristic Province.

Key Words: Edaphic endemism, gabbro, geobotany, plant nutrition, plant-soil relations, rare plants, soil chemistry.

Soil is an intermediary between bedrock and vegetation. The chemical composition of this biologically important layer is largely determined by the composition of underlying parent materials (Rajakaruna and Boyd 2008). Soil composition is a significant factor in plant ecology and evolution: various plant species have evolved specific traits, such as the ability to tolerate heavy metals or nutrient imbalances, as a result of natural selection in populations on particular soils (Kruckeberg 1986; O'Dell and Rajakaruna 2011). These traits influence plant physiology, distribution, and speciation, demonstrating that attention to soil parent materials is a vital part of botanical research. While certain edaphic systems, such as serpentine (Harrison and Rajakaruna 2011) and gypsum (Escudero et al. 2015; Moore et al. 2014), have been the subject of extensive study, gabbro has not received the same level of attention as a unique edaphic environment.

Gabbro is a mafic (magnesium- and iron-enriched) rock with mineralogy and chemistry that span the range between diorite and peridotite (Fig. 1). Gabbro soils develop from gabbro parent materials. They share many plant species with diorite soils and some with ultramafic soils (Whittaker 1960); several plant species character-

istic of ultramafic soils are also found on gabbro soils (Baldwin et al. 2012). Worldwide, the distribution of plant species and communities on gabbro soils have been addressed by Gertenbach (1978) and Peel et al. (2007) in South Africa, Marrs and Proctor (1978) in England, Dayton (1966) in North Carolina, Schmidt and Barnwell (2002) in South Carolina, and Buck (1964) in Oklahoma. These studies have generally noted the existence of distinctive plant communities on gabbro soils, and have either offered no explanation or speculated that the unique assemblage of species is due to unusual nutrient levels or soil types. Other studies have used gabbro as a "normal" substrate to which the vegetation of a serpentine substrate is contrasted (e.g., Adamson et al. 1993). In the California Floristic Province (CFP), the vegetation of gabbro soils has been discussed by Whittaker (1960), Hunter and Horenstein (1992), Oberbauer (1993), Tarp (1998), Tarp et al. (2002), Wilson et al. (2010), Burge and Manos (2011), Gogol-Prokurat (2011), and others.

In this paper we review the published literature concerning rocks, soils, and plants of gabbro outcrops in the CFP. We provide descriptions of gabbro rocks and soils, followed by an overview

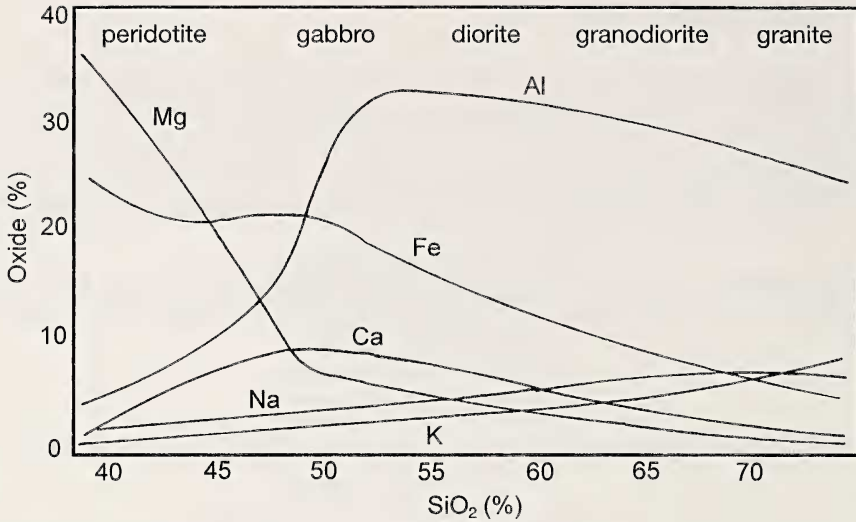


FIG. 1. Metal oxide concentrations in plutonic rocks, based on data in Le Maitre (1976).

of plant nutrition on gabbro soils. We then discuss hypotheses for the restriction of some taxa to gabbro soils and some possibilities for identifying the limiting properties of gabbro soils that might restrict the distributions of rare plants. Finally, we highlight gabbro areas in California where botanical research has been conducted, and provide a list of gabbro-endemic, rare, and otherwise interesting plants known to occur on gabbro in the CFP (Appendices 1 and 2).

OCCURRENCE AND COMPOSITION OF GABBRO

Gabbro is a plutonic igneous rock formed by the subterranean solidification of mafic magma. It is found in Precambrian layered complexes on continental platforms (e.g., the Canadian Shield), in more recent plutons in continental orogenic regions, and in the oceanic crust continuously produced at mid-ocean spreading centers. In the CFP, gabbro is widely distributed in Mesozoic plutons in the Sierra Nevada, Klamath Mountains, and Peninsular Ranges, and sparsely distributed in the eastern Transverse Ranges and the California Coast Ranges; gabbro also occurs in the western Mojave Desert, just outside the CFP (CGS 2010; Fig. 2).

Geologists characterize igneous rocks with regard to mineral composition and texture (Fig. 1). Chemically, gabbro is identical to basalt; unlike gabbro, basalt solidifies at the Earth's surface, cooling quickly to produce an aphanitic (small grained) texture. Gabbro has a phaneritic (large-grained) texture formed by the slow crystallization typical of plutonic rocks. It is composed predominantly of the minerals pyroxene, plagioclase that is more calcic (Ca-rich) than sodic (Na-rich), and either olivine or hornblende (Le Maitre 2002; Table 1). Olivine is a Fe-bearing

Mg-silicate, while hornblende is a silicate mineral containing Ca, Al, and Na in addition to Fe and Mg. Gabbro generally contains more clinopyroxenes (containing Ca) than orthopyroxenes (lacking Ca); the closely related rock norite is fundamentally gabbro dominated by orthopyroxenes. Silica (SiO₂) content in gabbro ranges from around 45% to about 54%; aluminum (Al) and magnesium (Mg) contents vary considerably in this range (Fig. 1), suggesting that broad ranges of these elements can be expected in gabbro rocks. And the range of possible chemical compositions is much broader for gabbro with olivine than for gabbro with hornblende (Alexander 2011). It is therefore inappropriate to assume that a gabbro outcrop or soil will conform to a generalized composition. Mineral contents or elemental concentrations must be measured at each gabbro site under study to be relevant to that site.

GABBRO SOILS

A brief note concerning terminology is warranted here. Although "gabbroic soils" would be a better term grammatically, we use the phrase "gabbro soils" here to be consistent with other geocological literature, in which "serpentine soils" is the accepted term for soils derived from serpentinite and other related rocks (see Rajakaruna et al. 2009).

Gabbro soils contain minerals inherited from their gabbro parent materials, and as a consequence are as diverse as the gabbro rocks discussed above. This diversity is compounded by the effects that climate, vegetation, exposure time, and topography may exert on soil formation (Kruckeberg 1986). For example, gabbro soils in the colder climate of the Klamath

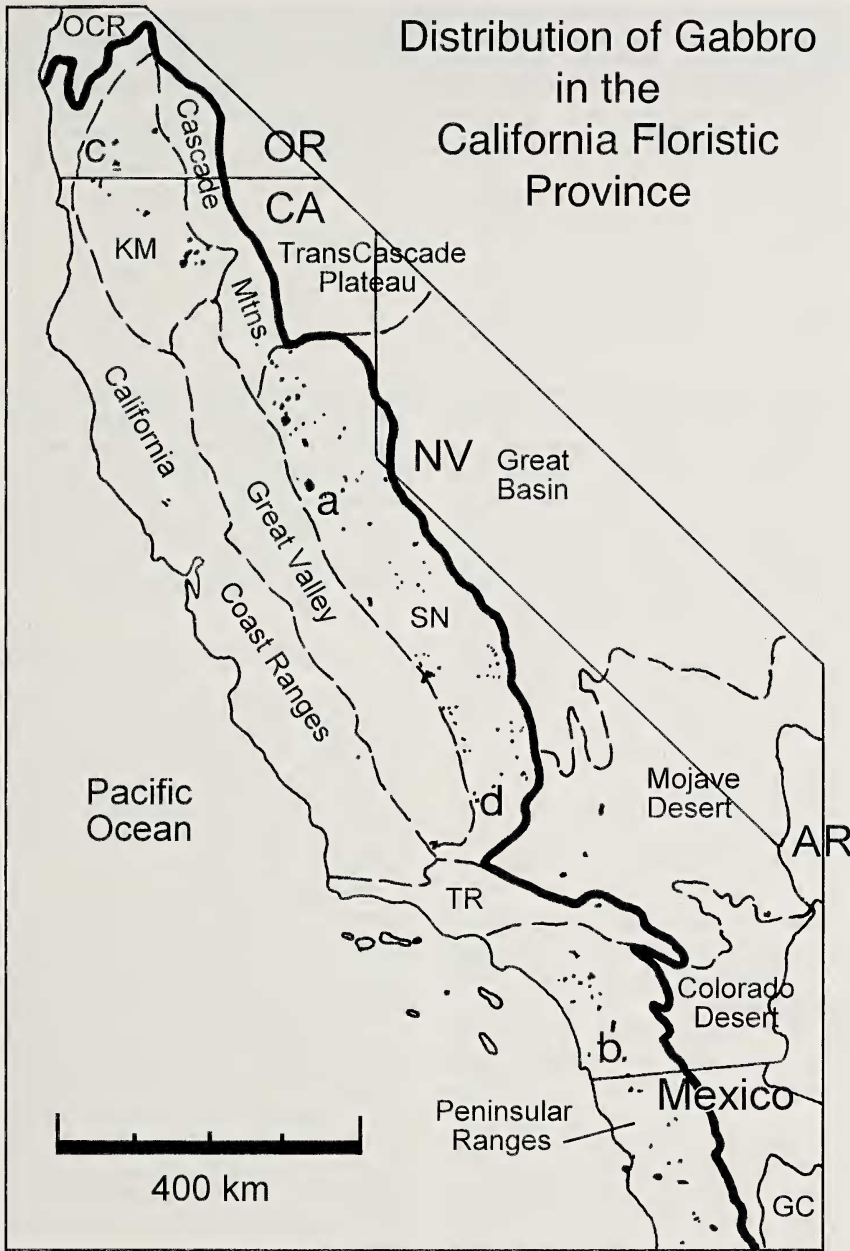


FIG. 2. Gabbro distribution in the California Floristic Province (CFP). Approximate border of CFP shown by bold line; note that it includes parts of California, Oregon, and Baja California. Geographic abbreviations: GC, Gulf of California; KM, Klamath Mountains; OCR, Oregon Coast Ranges; SN, Sierra Nevada; TR, Transverse Ranges. The following gabbro outcrops discussed in this paper are marked with an approximate position on the map: a, Pine Hill Intrusive Complex; b, Guatay Mountain and King Creek Research Natural Areas, c, Klamath-Siskiyou Mountains; d, Bodfish Piute Cypress Botanical Area. Map based on Gastil (1975), Jennings (1977), and Walker and McLeod (1991).

Mountains typically have less clay than gabbro soils in the warmer Peninsular Ranges (EBA, unpublished data).

Gabbro soils in the CFP are mostly Alfisols, with some Inceptisols and Mollisols, and a few Entisols (Soil Survey 1973; Soil Survey Staff 1999). They are in loamy-skeletal, fine-loamy,

clayey-skeletal, and fine families. Unlike granite, gabbro typically weathers to silt and clay rather than coarse grus. Therefore, gabbro soils are commonly less sandy and more silty and clayey than granite soils (Alexander 1993). Because gabbro is generally more Fe-rich than granitic rocks, gabbro soils are commonly redder than

TABLE 1. MAJOR MINERALS IN INTRUSIVE IGNEOUS ROCKS, FROM DOMINANT (+++) TO MINOR (+), OR ABSENT (—). Both extrusive volcanic and chemically equivalent intrusive plutonic rocks have the same, or similar, minerals; it is mainly the grain sizes that are different. ^a The major cations in alkali feldspars are Na and/or K. ^b Hornblende is a major element in hornblende gabbro, but a minor element in olivine gabbro. Data compiled from Le Maitre (2002).

Mineral	Peridotite	Gabbro	Diorite	Granodiorite	Granite
Quartz	—	—	—	++	+++
Alkali Feldspars ^a	—	—	+	++	+++
Calcic Feldspars	—	+++	++	+	—
Biotite	—	—	—	+	++
Hornblende ^b	—	+	+++	++	+
Pyroxenes	+++	++	+	—	—
Olivine	+++	+	—	—	—

granite soils. Granite soils that are reddish are more yellowish red, while gabbro soils are more brownish red. Gabbro has more basic cations, especially Ca and Mg, than granitic rocks, and commonly less Al (except gabbro with much hornblende or feldspar); consequently, the cation-exchange complexes of gabbro soils generally have larger percentages of basic cations (greater base saturation) than the cation-exchange complexes of granitic soils. Soil pH is commonly higher in gabbro soils than in granite soils, mainly because base saturation is commonly higher in the former. Gabbro soils in the CFP are most commonly slightly to moderately acidic (Soil Survey 1973; Alexander 2011).

Gabbro soils differ from ultramafic soils (such as soils derived from serpentine) in having more Ca and much less Mg, as reflected in molar Ca/Mg ratios $\gg 1$ in surface soils and > 1 in subsoils (Alexander 2011), whereas the ratios in serpentine soils are generally < 1 in surface soils and $\ll 1$ in subsoils (Alexander et al. 2007). First transition elements that can be toxic to plants (Cr, Co, and Ni) are much less concentrated in gabbro soils than in serpentine soils (Table 2). Nevertheless, some soils developed

from olivine gabbro may have elemental concentrations nearer to those of serpentine soils than to average gabbro soils. Serpentine soils are known to be harsh environments with high rates of endemism (Safford et al. 2005; Anacker 2011), so understanding the similarities between serpentine soils and gabbro soils may help us better understand gabbro endemism.

PLANT NUTRITION IN GABBRO SOILS

Plants require C, H, O, N, and K in large amounts, Ca, Mg, P, S, Cl, Fe, B, and Mn in moderate amounts, Cu, Na, and Zn, in small amounts, and Mo, Co, and Ni in minute amounts for their growth (Marschner 1995). Several of these elements pertain directly to gabbro soils and are discussed below.

Nitrogen that plants acquire as NO_3^- must be reduced to NH_4^+ with nitrogen reductase, an enzyme containing Mo. Although Mo has been reported to limit plant growth in serpentine soils (Walker 1948; Alexander et al. 2007), there is no research suggesting that it is a limiting element in gabbro soils. According to Vinogradov (1962), the average content of Mo in gabbro is significantly greater than that of ultramafic rocks or diorite. However, as stated previously, average values have little significance for individual gabbro outcrops, and we know of no data on the variability of Mo contents in gabbro across California.

Average Ca contents are high in gabbro compared to more silicic igneous rocks (Table 2, Fig. 1), but the range in compositions varies greatly. Whereas molar exchangeable Ca/Mg ratios in olivine gabbro soils may be so low (possibly < 0.7) that plants may be unable to uptake sufficient Ca, the exchangeable Ca/Mg ratios in hornblende gabbro soils may be so high that plants cannot obtain sufficient Mg.

Potassium exists at low concentrations in gabbro parent material (Le Maitre 1976). In an investigation of three gabbro soils in the Pine Hill area of the Sierra Nevada and three in the Cuyamaca-Guatay area of the Peninsular Ranges (Alexander 2011), the Pine Hill soils contained

TABLE 2. FIRST TRANSITION ELEMENTS (ATOMIC NUMBERS 21–30) AND MOLYBDENUM (MO) IN IGNEOUS ROCKS FROM WORLDWIDE AVERAGES OF VINOGRADOV (1962), WHO INCLUDED ANDESITE WITH DIORITE, BASALT WITH GABBRO, AND DUNITE WITH PERIDOTITE.

Element	Diorite concentration (ppm)	Gabbro concentration (ppm)	Peridotite concentration (ppm)
Sc	2	24	5
Ti	8000	9000	300
V	100	200	40
Cr	50	200	2000
Mn	1200	2000	1500
Fe	58,500	85,600	98,500
Co	10	45	200
Ni	55	160	2000
Cu	35	100	20
Zn	72	130	30
Mo	0.3	1.4	0.9

less K than the Cuyamaca-Guatay soils. The Cuyamaca-Guatay soils had parent materials with considerable hornblende, which is a potential source of K, whereas the Pine Hill soil parent materials were replete with pyroxenes that lack K.

Phosphorus is typically low in plutonic rocks (Le Maitre 1976), and may be particularly low in gabbro (Barral et al. 2011). Dust from the atmosphere may be a major source of P in gabbro soils, just as proposed for serpentine soils (Alexander et al. 2007). Phosphorus derived from the weathering of soil parent material or from dust is utilized by plants and accumulates in soil organic matter. Plants continuously recycle it and little is lost from undisturbed soils. Alexander (2011) showed that the amounts of P in gabbro soils of the Pine Hill and Cuyamaca-Guatay areas are related to amounts of soil organic matter. The bioavailability of soil P is closely related to soil pH, with P fixed as Ca-phosphates at high pH and adsorbed on Fe and Al-oxides at low pH (Frossard et al. 1995). The pH values of gabbro soils in the CFP are generally in or near the 6 to 7 range (Soil Survey 1973) where soil P is most available to plants (as mono- or di-hydrogen phosphates; Frossard et al. 1995). Available P varies seasonally along with microbial activity and plant uptake (Sharpley 2000); measured values of "available" P may also depend heavily on the type of extraction used.

Sulfur occurs in minute amounts in gabbro (about 0.3 g/kg in mafic rocks according to Vinogradov 1962), mainly in sulfides such as pyrite (FeS_2). Most of the S in gabbro soils is deposited from atmospheric gasses and from sulfates in precipitation. The major sources of atmospheric S are volcanic activity and the burning of fossil fuels and vegetation. Plants do not require much S and it is recycled back into plants as sulfates from the decomposition of plant detritus. Sulfur is more mobile than P in soils and deficiencies can occur in highly leached soils (Marschner 1995), but S deficiencies are unlikely to occur in gabbro soils of the CFP (Alexander 2007; but see Burge and Manos 2011).

Copper, Mn, and Zn contents in gabbro are higher than the contents in other kinds of plutonic rocks, and like other mafic and ultramafic rocks gabbro contains ample amounts of Fe, Co, Ni, and Mg (Table 2). No plant nutrient deficiencies would be expected for these elements in gabbro soils or for other micronutrients such as Cl, B, and Na.

To summarize the soil elemental data: K is low in some gabbro soils and may be a limiting nutrient, but this varies within and between soils or outcrops. P may be a limiting nutrient, depending on the pH of the site. Bioavailability of Ca and Mg varies with the type of gabbro. Other nutrients do not seem to be scarce in

gabbro soils, and although the concentrations of some micronutrients are higher in gabbro than in other plutonic rocks, metal toxicity does not seem to be an issue.

THE EDAPHIC FACTOR IN PLANT DISTRIBUTIONS ON GABBRO SOILS

Various authors have cited soil nutrient levels, soil moisture, slope position, slope aspect, and other factors as being important in the distributions of plants within an area of gabbro soil. Some of these factors are discussed below; which factor is most important almost certainly depends on the particular species in question.

Gabbro soils that support rare plants exhibit a broad range of physical characteristics; similar ranges of physical characteristics are found in many Alfisols and Mollisols of California with other parent materials (Soil Survey 1973). It has therefore been assumed that soil chemistry, rather than physical characteristics, is responsible for unique plant associations found on gabbro soils. This assumption was implicit in Hunter and Horenstein (1992) and other references cited in the introduction. However, Alexander (2011) found that adjacent gabbro soils, which supported or lacked rare plants at the Pine Hill and Cuyamaca-Guatay areas, did not differ significantly in important plant nutrients such as K and P.

There is great variation in the chemistry of soils derived from gabbro, and plant distributions on gabbro soils are likely dependent on more than soil chemistry (Gogol-Prokurat 2011). Wilson et al. (2010) investigated the distributions of eight rare plant species on gabbro in the Pine Hill area of El Dorado County, and all but one of those species occurred in different plant communities and microclimates. They suggested that slope aspect was one of the key factors affecting the distribution of these species. Two of the Pine Hill species, *Calystegia stebbinsii* Brummitt (Convolvulaceae) and *Packera layneae* (Greene) W.A. Weber & A. Löve (Asteraceae), occur on both gabbro and serpentine soils, but on no soils with other parent materials. Another plant that grows only on gabbro and serpentine soils in the Klamath Mountains is *Frangula californica* (Eschsch.) A. Gray subsp. *occidentalis* (Howell ex Greene) Kartesz & Gandhi (Rhamnaceae) (Alexander 2014).

Another intriguing phenomenon is the occurrence of plants on some gabbro soils but not on nearby gabbro soils with similar microclimates; this problem of distribution was addressed by Burge and Manos (2011, but also see Alexander 2012). Distributions of certain rare plants are spotty even on the same kinds of gabbro soils, and many of the same rare plants appear on diverse kinds of gabbro soils. In San Diego County, for example, *Hesperocyparis stephensonii*

(C.B. Wolf) Bartel (Cupressaceae) was found on both a brown Alfisol (Haploxeralf) and a red Alfisol (Rhodoxeralf) with gabbro parent materials (Alexander 2011). Considerably lower exchangeable Ca in the brown Alfisol may be more of a limitation for the cypress than the physical characteristics that differentiate between the Haploxeralf and Rhodoxeralf great groups. The focus of geobotanical investigations should be on soil properties rather than on soil classification.

Burge and Manos (2011) suggested that the gabbro endemic *Ceanothus roderickii* W. Knight evolved from a population of *C. cuneatus* (Hook.) Nutt. var. *cuneatus* that was locally adapted to nutrient-poor gabbro soils in the Pine Hill area. They noted that *C. roderickii* is generally found on steeper slopes with less developed soil, while *C. cuneatus* var. *cuneatus* is predominantly found near slope bottoms. It is still not clear why *C. roderickii* or many of the other Pine Hill endemics remain restricted to gabbro alone.

In terms of strict endemism, there are fewer than 10 gabbro endemics in California. The gabbro-endemic taxa at Pine Hill and elsewhere (Appendix 1) comprise a tree, shrubs, and forbs; many come from high-diversity genera in the CFP flora (e.g., *Ceanothus* L.), while others do not (e.g., *Wyethia* Nutt.). They are all perennials (Baldwin et al. 2012); they are probably all neoendemics (Harrison 2014). Further study of the age and edaphic tolerances of these species will be required before any definite statements can be made about gabbro endemism or other unusual plant distributions seen on gabbro soils.

ON THE RELATIONSHIP BETWEEN PLANT DISTRIBUTION ON GABBRO AND SERPENTINE SOILS

As we have mentioned previously, chemical and mineralogical similarities exist between gabbro (particularly olivine gabbro) and serpentine. Furthermore, the two rock types are often found in close proximity (Alexander et al. 2007; Lyons et al. 2010; Wilson et al. 2010). As discussed elsewhere in this paper, certain “gabbro endemics” have been reported from nearby serpentine sites, and vice versa for “serpentine endemics” on gabbro. This leads to an as-of-yet unresolved question: are certain serpentine endemics found on gabbro because it is sufficiently similar to serpentine in chemistry, nutrition, ecological competition, or some other factor to allow limited colonization, or are the taxa in question not “endemic” to serpentine at all, but to some feature shared between the two substrate types?

Because gabbro produces soils that are less “harsh” than serpentine soils, it makes sense that serpentine endemism is a more dramatic (and prevalent) phenomenon than gabbro endemism.

But since olivine gabbro is chemically somewhat similar to serpentine, vegetation similarities might be expected between the two; likewise, fewer vegetation similarities would be expected between hornblende gabbro and serpentine. These areas need further study before conclusions can be reached on the relationship between plant distribution patterns on gabbro and serpentine soils.

NOTABLE GABBRO OUTCROPS IN THE CALIFORNIA FLORISTIC PROVINCE

Bodfish Piute Cypress Botanical Area

This protected area in Sequoia National Forest is located south of Lake Isabella in Kern County. Gabbro soils at this site support *Streptanthus cordatus* Nutt. var. *piutensis* J. T. Howell (Brassicaceae), a rare plant known only from Kern County (Greene and Sanders 1998). This taxon has not been labeled a strict gabbro endemic, as a few individuals have been reported from off gabbro. However, considering that most *Streptanthus* Nutt. spp. exhibit some degree of serpentine affinity (Baldwin et al. 2012), it would not be inconceivable for *S. cordatus* Nutt. var. *piutensis* to be a gabbro endemic. This taxon requires more thorough geocological study.

Guatay Mountain and King Creek Research Natural Areas

Areas of hornblende gabbro are located in San Diego County, California, within Cleveland National Forest. They were investigated (as the “Cuyamaca-Guatay area”) by Alexander (2011). *Hesperocyparis stephensonii*, a gabbro-endemic conifer, occurs only at the King Creek site, and within that site is restricted to the deeper, wetter soils at the base of slopes, rather than drier, steeper soils further upslope (Keeler-Wolf 1990). The Viejas Mountain Research Natural Area, another incidence of gabbro soil in Cleveland National Forest known to support at least one rare plant species (USFS s.d.), was not included in Alexander’s 2011 study. Species lists for all three areas have been compiled in unpublished Forest Service reports.

Pine Hill Preserve

Located in El Dorado County in the Sierra Nevada foothills, the Pine Hill Preserve has received considerable attention from California botanists and soil scientists (see Hunter and Horenstein 1992; Wilson et al. 2010; Alexander 2011; Burge and Manos 2011). A comprehensive survey of the area (Wilson et al. 2010) lists 741 vascular plant taxa, of which 634 taxa occur on the preserve’s olivine gabbro. These include two species – *Quercus durata* Jeps. and *Streptanthus*

polygaloides A. Gray – that are described as narrow or strict serpentine endemics (Safford et al. 2005). *Chlorogalum grandiflorum* Hoover (a broad serpentine endemic) and *Packera layneae* (a strong serpentine indicator) also grow on gabbro at Pine Hill.

Several species are endemic to this area, including *Calystegia stebbinsii*, *Ceanothus roderickii*, *Fremontodendron decumbens* R. M. Lloyd, *Galium californicum* Hook. & Arn. subsp. *sierrae* Dempster & Stebbins, and *Wyethia reticulata* Greene (Brummitt 1974; Hunter and Horenstein 1992; Ayres and Ryan 1999; Wilson et al. 2010). For discussions of the fire and dispersal ecology of *F. californicum* subsp. *decumbens* and *C. roderickii*, see Boyd and Serafini (1992) and Boyd (1994, 1996, 2001, 2007). For genetic information on the two aforementioned species and *W. reticulata*, see Ayres and Ryan (1999), Kelman et al. (2006) and Burge and Manos (2011). It is not clear why the Pine Hill site harbors most of California's gabbro endemics, although habitat complexity has been suggested as a possible reason.

It would be tempting to ascribe the greater number of serpentine indicator plants observed by Alexander (2011) at Pine Hill versus the Guatay Mountain and King Creek RNAs to the presence of olivine gabbro (which is chemically closer to serpentinite) at Pine Hill versus the presence of hornblende gabbro at Guatay Mountain and King Creek. However, the Pine Hill intrusive complex contains a perimeter of ultramafic rocks around the gabbroic pluton, while the Guatay Mountain and King Creek areas do not (CGS 2010). Further work is needed to isolate substrate effects on distribution from dispersal effects on distribution.

Diablo Range

In a floristic report of the Mount Hamilton region of the San Francisco Bay Area, Sharsmith (1945) said very little about gabbro, reporting only that soils derived from gabbro are infertile. We presume that she was referring to a small gabbro outcrop near what is now Frank Raines Regional Park, an off-highway vehicle area, since there are no other gabbro outcrops near Mount Hamilton (CGS 2010). This outcrop is adjacent to a much larger area of serpentine, and could be an interesting site in which to compare the vegetation of the two parent materials.

Klamath-Siskiyou Mountains

Whittaker (1960) investigated plant distributions along a moisture gradient on diorite, gabbro, and serpentine soils in northern California and southern Oregon, emphasizing the individuality of species' responses to different soils

and describing gabbro plant communities that were intermediate between those of granitic and ultramafic soils. He reported that gabbro forests were more open and less dominated by *Pseudotsuga menziesii* (Mirb.) Franco than nearby diorite forests, and that stream banks were more vegetated on gabbro than on either serpentine or diorite; however, a later analysis of his data by Grace et al. (2011) found that overall species richness was lowest on gabbro. Several species were mostly absent on diorite but were major elements of gabbro communities: *Umbellularia californica* (Hook. & Arn.) Nutt. (which also occurs at Pine Hill [Wilson et al. 2009]), *Arctostaphylos cinerea* Howell, *Frangula californica* subsp. *occidentalis* (Howell) Kartesz & Gandhi, and *Vaccinium ovatum* Pursh. Four species were found on gabbro only: *Luina hypoleuca* Benth., *Darmera peltata* (Torrey) Voss, *Epipactis gigantea* Hook., and *Erigeron cervinus* E. Greene. Damschen et al. (2010) resurveyed Whittaker's serpentine and diorite sites and documented a loss of species diversity, especially endemic species diversity; they ascribed this shift to climate change. Whittaker's gabbro sites were not resurveyed because a 2002 fire burned the entire gabbro study area.

FUTURE DIRECTIONS

The first step towards identifying soil properties responsible for selective distributions of plants on some gabbro soils and not on others would be to comprehensively analyze many gabbro surface and subsoils with similar microclimates throughout an area. Analyses of both surface soils and subsoils sampled below 25 or 30 cm are important, to account for differences in rhizosphere depth between plant species. Surface soil properties can be influenced greatly by recent disturbance and differences in plant cover that may be unrelated to the properties of the soil as a whole. Following soil sampling and analyses, comparisons of the properties of soils supporting rare plants with the properties of soils lacking rare plants may provide some clues about those soil properties that limit the distributions of the plants.

Gabbro endemism in vascular plants is poorly studied in comparison to serpentine endemism. Reciprocal transplants and common garden studies with plants known only from gabbro could help to clarify the nature of gabbro endemism, provided that these studies examine a variety of variables such as soil type and structure, slope and aspect, and soil chemistry. Such studies should investigate whether purportedly gabbro endemic taxa can survive on serpentine or granite/diorite soils if given the opportunity. The reverse (whether serpentine endemics can survive on gabbro) should also be tested.

To the best of our knowledge no one has published a survey of bryophytes on gabbro outcrops in California. One such survey in South Carolina (Bowe and Rayner 1993) found moisture to be a more important factor than bedrock type in determining species composition. However, at least one rare moss species in California is endemic to serpentine: *Pseudoleskella serpentinensis* P. Wilson & Norris has been reported from serpentine in the Klamath-Siskiyou area (Malcolm et al. 2009). No comprehensive work has been done on the lichens of gabbro outcrops in California. As serpentine rocks in the CFP have been shown to support unique lichen assemblages (Rajakaruna et al. 2012), a study of gabbro lichens could be worthwhile. Comparisons should also be made between mycorrhizal communities on gabbro and other unique substrates, such as serpentine (Southworth et al. 2014).

Gervais and Shapiro (1999) discussed edaphic endemism (as a consequence of plant specificity) in Sierra Nevada Lepidoptera. They focused on serpentine, but did note populations of "serpentine endemic" butterflies and skippers on gabbro. Further entomological insight could follow from a better understanding of why certain plants live on certain gabbro soils.

In terms of conservation, work should be done to model the effects that climate change may have on the plants of gabbro soils, as has been done for serpentine (see Damschen et al. 2012). Other threats to these plants should also be regularly assessed. One could speculate that the plants restricted to gabbro soils face greater conservation threats than serpentine plants because gabbro lacks the public awareness that serpentine has earned as California's state rock.

Further work should be done to map the distributions of olivine and hornblende gabbro in the CFP, and to integrate this knowledge with research in gabbro vegetation ecology. Although endemism to particular rock types is a paradigm in geocology, chemical variation can cause significant variation in vegetation within one "type" of rock (Hahm et al. 2014). Differences between the gabbro outcrops documented by Alexander (2011) may be attributable to rock chemistry differences, and we believe that this could be a fertile area of research in the future.

CONCLUSIONS

Although gabbro has not received as much attention as serpentine, it is a unique edaphic system that poses several interesting questions concerning endemism, species distributions, and edaphic ecology. Soil chemistry, soil moisture, topography, and proximity to serpentine bedrock may all play a role in the formation of a unique gabbro vegetation, although much more work remains to be done before gabbro endemism is

understood on either a broad or a species-by-species basis. Continued research into the evolution and ecology of gabbro endemic taxa should be an important facet of geobotanical investigations in the California Floristic Province.

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APPENDIX 1. RARE PLANTS REPORTED FROM GABBRO SOILS OF THE CALIFORNIA FLORISTIC PROVINCE

This appendix summarizes the taxa that have been (a) reported to occur on gabbro in the CFP, and (b) have a rarity status according to the California Native Plant Society and/or a serpentine indicator rating in Safford et al. (2005). An exhaustive search of California herbaria would almost certainly reveal additional taxa that belong on this list, although such a search is not within the scope of this paper (to that end, though, we encourage herbaria to make their online collections databases more easily searchable by ecological data).

Headings. Serp. = serpentine affinity as reported in Safford et al. (2005); CA = California listing status as reported in CNPS (2013); FE = federal listing status as reported in CNPS (2013); CNPS = rare plant rank as reported in CNPS (2013). Gabbro endemic taxa are in bold text; potential gabbro endemics are followed by a bold question mark in parentheses (?).

Literature sources indicate where each taxon is reported on gabbro: a. Alexander et al. 2007; b. Alexander (2011); c. Alexander (2014a); d. Ayres and Ryan (1999); e. Baldwin et al. (2012); f. Boyd and Ross 1997; g. Burge and Manos (2010); h. CNPS (2013); i. Greene and Sanders (1998); j. Simpson et al. 2013; k. Hirshberg and Levin 1988; l. Hunter and Horenstein 1992; m. Levin and Hirshberg 1991; n. Preston (2006b); o. USDA s.d.; p. Whittaker (1960); q. Beauchamp (1986).

Family	Taxon	Source	Serp.	Rarity		
				CA	FE	CNPS
Apiaceae	<i>Lomatium howellii</i> (S. Watson) Jeps.	p	6.1	-	-	4.3
Asteraceae	<i>Arnica spathulata</i> Greene	p	5.5	-	-	4.3
	<i>Erigeron cervinus</i> Greene	p	3.3	-	-	4.3
	<i>Packera ganderi</i> (T.M. Barkley & R.M. Beauch.) W.A. Weber & A. Löve	e	-	CR	-	1B.2
	<i>Packera layneae</i> (Greene) W.A. Weber & A. Löve	b, l	4.9	CR	FT	1B.2
	<i>Wyethia reticulata</i> Greene	b, d	-	-	-	1B.2
Boraginaceae	<i>Cryptantha wigginsii</i> I.M. Johnst.	j	-	-	-	1B.2
Brassicaceae	<i>Sibaropsis hammittii</i> S. Boyd & T.S. Ross	f	-	-	-	-
	<i>Streptanthus cordatus</i> Nutt. var. <i>piutensis</i> J. T. Howell (?)	i	-	-	-	1B.2
Cistaceae	<i>Crocathemum suffrutescens</i> (B. Schreib.) Sorrie	l	-	-	-	3.2
Convolvulaceae	<i>Calystegia stebbinsii</i> Brummitt	l	-	CE	FE	1B.1
Crassulaceae	<i>Sedum laxum</i> (Britton) A. Berger subsp. <i>heckneri</i> (M. Peck) R.T. Clausen	e, g	3.5	-	-	4.3
Cupressaceae	<i>Hesperocyparis forbesii</i> (Jeps.) Bartel	b	-	-	-	1B.1
	<i>Hesperocyparis nevadensis</i> (Abrams) Bartel	i	-	-	-	1B.2
	<i>Hesperocyparis stephensonii</i> (C. B. Wolf) Bartel	b	-	-	-	1B.1
Cyperaceae	<i>Carex obispoensis</i> Stacey	h	4.9	-	-	1B.2
Ericaceae	<i>Arctostaphylos klamathensis</i> S. W. Edwards, Keeler-Wolf & W. Knight	h	3.9	-	-	1B.2
Lamiaceae	<i>Acanthomintha ilicifolia</i> A. Gray	o	1.3	CE	FT	1B.1
	<i>Clinopodium chandleri</i> (Brandege) P.D. Cantino & Wagstaff	h	-	-	-	1B.2
	<i>Lepechinia ganderi</i> Epling	h	-	-	-	1B.3

APPENDIX 1. CONTINUED.

Family	Taxon	Source	Serp.	Rarity		
				CA	FE	CNPS
	<i>Monardella hypoleuca</i> A. Gray subsp. <i>lanata</i> (Abrams) Munz	a	-	-	-	1B.2
	<i>Salvia sonomensis</i> Greene	b	1.6	-	-	-
Liliaceae	<i>Calochortus dunnii</i> Purdy	g	-	CR	-	1B.2
	<i>Chlorogalum grandiflorum</i> Hoover	b, l	5.2	-	-	1B.2
Malvaceae	<i>Fremontodendron decumbens</i> R. M. Lloyd	e, l	-	CR	FE	1B.2
	<i>Fremontodendron mexicanum</i> Davidson	h	-	CR	FE	1B.1
	<i>Sidalcea elegans</i> Greene	p	-	-	-	3.3
Onagraceae	<i>Clarkia delicata</i> (Abrams) A. Nelson & J. F. Macbr.	h	-	-	-	1B.2
	<i>Epilobium minutum</i> Lindl. ex Lehm.	m	2	-	-	-
Orchidaceae	<i>Cypripedium californicum</i> A. Gray	p	4.5	-	-	4.2
Orobanchaceae	<i>Kopsiopsis hookeri</i> (Walp.) Govaerts	p	-	-	-	2B.3
Picodendraceae	<i>Tetracoccus dioicus</i> Parry	a	-	-	-	1B.2
Phrymaceae	<i>Mimulus clevelandii</i> Brandegee	h	-	-	-	4.2
Pteridaceae	<i>Aspodotis densa</i> (Brack.) Lellinger	k	3.4	-	-	-
Ranunculaceae	<i>Delphinium hesperium</i> A. Gray subsp. <i>cuyamaca</i> (Abrams) F. H. Lewis & Epling	q	-	CR	-	1B.2
Rhamnaceae	<i>Ceanothus ophiochilus</i> S. Boyd, T. S. Ross & Arnseth	h	-	CE	FT	1B.1
	<i>Ceanothus otayensis</i> McMinn	h	-	-	-	1B.2
	<i>Ceanothus roderickii</i> W. Knight	e, g, l	1.7	CR	FE	1B.2
	<i>Frangula californica</i> (Eschsch.) A. Gray subsp. <i>occidentalis</i> (Howell ex Greene) Kartesz & Gandhi	c	6	-	-	-
Rosaceae	<i>Adenostoma fasciculatum</i> Hook. & Arn.	b	1.3	-	-	-
	<i>Chamaebatia australis</i> (Brandegee) Abrams	h	-	-	-	4.2
	<i>Horkelia truncata</i> Rydb.	h, q	-	-	-	1B.3
Rubiaceae	<i>Galium californicum</i> Hook. & Arn. subsp. <i>sierrae</i> Dempster & Stebbins	b, l	-	CR	FE	1B.2
Ruscaceae	<i>Nolina cismontana</i> Dice	h	-	-	-	1B.2
	<i>Nolina interrata</i> Gentry	e, h	-	CE	-	1B.1
Sarraceniaceae	<i>Darlingtonia californica</i> Torr.	p	4.1	-	-	4.2
Themidaceae	<i>Brodiaea sierrae</i> R.E. Preston	n	-	-	-	4.3

APPENDIX 2. SPECIES MENTIONED IN THIS APPENDIX DO NOT MEET THE RARITY OR SERPENTINE AFFINITY CRITERIA FOR INCLUSION IN APPENDIX 1, BUT HAVE BEEN NOTED IN THE LITERATURE TO HAVE AN OCCASIONAL AFFINITY FOR GABBRO SOILS IN SOME PART OF THEIR RANGE. Literature sources: a. Baldwin et al. (2012); b. Beauchamp (1986); c. Oberbauer (1993); d. Preston (2006a).

Family	Taxon	Source
Brassicaceae	<i>Caulanthus heterophyllus</i> (Nutt.) Payson	b
Hypericaceae	<i>Hypericum concinnum</i> Benth.	a
Poaceae	<i>Calamagrostis koelerioides</i> Vasey	b
Rhamnaceae	<i>Ceanothus foliosus</i> Parry	c
Rosaceae	<i>Rubus glaucifolius</i> Kellogg	c
Themidaceae	<i>Brodiaea minor</i> (Benth.) S. Watson	d